



## The use of relative abundance patterns to discriminate among niche apportionment processes

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**Abstract:** Several different stochastic models of niche apportionment have been proposed to explain the structure of species' relative abundance patterns within communities. Here I deal with the converse issue, i.e., whether it is possible to infer past niche apportionment processes from current relative abundance patterns.

Using Monte Carlo methods, I constructed relative abundance patterns for many 'communities' of four to 28 species based on five common niche apportionment models (Dominance Decay, Dominance Preemption, MacArthur Fraction, Random Assortment and Random Fraction). The relative abundance patterns of these individual communities were compared by a best-fit test against those expected to emerge over many replications of the different models. The proportion of instances that the past structuring processes were correctly identified was generally quite low for four-species communities, and was inconsistent across niche apportionment models. For 28-species communities, the probability of correct model identification was greater for all models, but remained inconsistent across models (indicating a persistent identification bias). In a second analysis, I constructed relative abundance distributions for many four-species communities, each composed of seven replicates. In this example (the structure of which was chosen to mirror that of a recently published study), the probability of correct identification was greater than for unreplicated four-species communities, but did not approach 1.0 for any model, and was once again inconsistent across models.

These results indicate that in many cases it is not possible to elucidate past ecological structuring processes from current relative abundance patterns alone. Attempts to use such patterns to distinguish among different types of niche apportionment should therefore be confined to situations with very high species richness and/or community replication, the specifics of which must be assessed on a case-by-case basis.

**Abbreviations:** DD-Dominance Decay, DP-Dominance Preemption, MF-MacArthur Fraction, RA-Random Assortment, RF-Random Fraction.

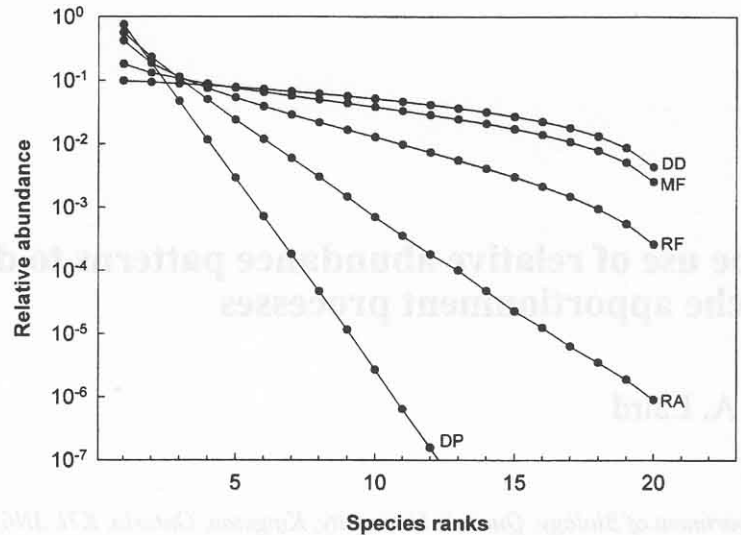
### Introduction

Patterns of relative abundance are a critical, yet understudied component of species diversity in ecological communities. Historically, the models for fitting relative abundance distributions (in which the relative abundance for each species in a community is plotted [log scale] versus its abundance rank; e.g., Fig. 1) can be divided into two main categories, those based on statistics and information theory, and biological models (cf. Tokeshi 1990). Deterministic statistical models, such as the Log-series model (Fisher et al. 1943), the Lognormal model (Preston 1948) and others (see Tokeshi 1999) may provide good fit to empirical data (e.g., Wilson 1991, Watkins and Wilson

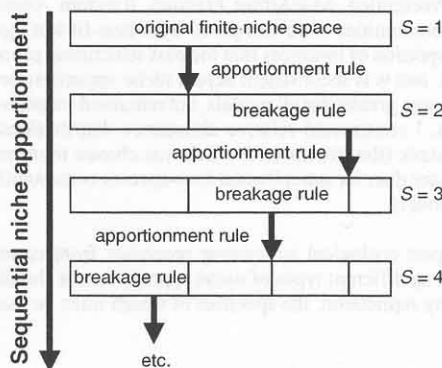
1994, Wilson et al. 1996). Yet, while authors have often attempted to attribute biological meaning to these statistical models, they are generally considered to be more useful for describing, rather than explaining, patterns in species abundance (Tokeshi 1990, Wilson 1991). However, for the purpose of understanding ecological assembly rules (see Weiher and Keddy 1999, Wilson 1999) and the ways that diversity is structured in natural communities, a mechanistic understanding of the underlying processes that give rise to such patterns would be invaluable.

To this end, Tokeshi (1990, 1993, 1999) proposed a series of biological models based on niche apportionment and inspired by the earlier work of MacArthur (1957). These models, based on the familiar 'broken stick' anal-

**Figure 1.** Expected (i.e., mean) relative abundance distributions (also known as rank abundance plots or dominance/diversity curves) based on five models of sequential niche apportionment: Dominance Decay (DD), MacArthur Fraction (MF), Random Fraction (RF), Random Assortment (RA) and Dominance Preemption (DP). Each relative abundance distribution was calculated for simulated communities of 20 species, although in the case of the Dominance Preemption model, only the first 12 ranks are displayed.



ogy, envision a finite niche space (i.e., a resource gradient represented by a one-dimensional 'stick'), divided and subdivided by the species that compose the community or assemblage of interest. There are two ways of interpreting niche apportionment models, in ecological terms (sequen-



**Figure 2.** Schematic diagram for sequential niche apportionment models (cf. Tokeshi 1993, 1999) for species richness  $S = 1$  to 4. A finite niche space is divided among species using two rules: (1) Apportionment rule – determines the fraction of niche space that each successive colonizer captures from a previous colonizer. (2) Breakage rule – determines which of the current niche fragments will be invaded by the next colonizer. The fraction of niche space occupied by a species is proportional to its relative abundance in the community. Specific combinations of different apportionment and breakage rules define the various sequential niche apportionment models that have been proposed. For example, this diagram depicts the Dominance Decay model. The apportionment rule is 'random' (see Table 1) so the fraction of niche space each successive colonizer captures from a previous colonizer is determined randomly. The breakage rule is 'Largest fragment is broken next' (Table 1) so at each step, the largest fragment is the one that gets subdivided.

tial colonization) or in evolutionary terms (where differences in competitive ability lead to dominance control) (Pielou 1975). Here I follow the ecological perspective (sequential niche apportionment models) for two reasons: First, it is easy to visualize graphically (Fig. 2), and second, it is the perspective used in recent treatments (Tokeshi 1999, Mouillot and Wilson 2002). The relative abundance patterns predicted by the niche apportionment models are the same regardless of whether their ecological or evolutionary interpretations are emphasized.

There are three main assumptions common to the sequential niche apportionment models: (1) Species colonize sequentially, with each successive colonizer capturing a fragment of niche space previously occupied by an earlier colonizer. The size of the fragment depends on an 'apportionment rule' (Bersier and Sugihara 1997). (2) The identity of the niche fragment that the next colonizer in an assemblage will subdivide depends on a 'breakage rule' (Bersier and Sugihara 1997). (3) A species' abundance in an assemblage is proportional to the fraction of total niche space it has captured (Tokeshi 1993). Different sequential niche apportionment models (e.g., Dominance Decay, MacArthur Fraction, Random Fraction, Random Assortment and Dominance Preemption) are produced by varying the apportionment and breakage rules (Table 1 provides a summary of these rules; see Tokeshi (1999) for a complete description and summary of ecological interpretations). Consider, for example, the Dominance Decay model (Fig. 2): The apportionment rule is 'random'; i.e., the size of the new fragment carved out of an existing fragment is determined randomly. For the same model, the breakage rule is 'largest fragment is broken next'; i.e., the largest fragment at any given moment will be the next one to be subdivided. The MacArthur Fraction model, on

**Table 1.** Various sequential niche apportionment models as defined by their apportionment rule (which determines the size of the fraction of niche space that new colonizers capture) and breakage rule (which determines which existing niche fragment new colonizers subdivide). All models described follow the additional assumption that the proportion of niche space captured by a colonizer is proportional to that colonizer's relative abundance.

Model	Apportionment rule	Breakage rule
Dominance Decay <sup>a</sup>	Random	Largest fragment is broken next
MacArthur Fraction <sup>a, b</sup>	Random	Fragment to be broken next chosen at random, weighted by fragment size
Random Fraction <sup>a</sup>	Random	Fragment to be broken next chosen at random (unweighted)
Random Assortment <sup>a</sup>	Random	Size of each fragment is determined randomly and is independent of all other fragment sizes
Dominance Preemption <sup>a</sup>	Random	Smallest fragment is broken next

<sup>a</sup> Tokeshi (1990)

<sup>b</sup> sequential niche apportionment equivalent of MacArthur's (1957) Broken Stick model

the other hand, has the same apportionment rule, yet its breakage rule is 'fragment to be broken next chosen at random, weighted by fragment size' (Table 1), meaning that the probability that any given fragment will be the next to be broken is proportional to its size (i.e., large fragments are more likely to be subdivided than small fragments). Models with similar apportionment and/or breakage rules will produce similar relative abundance distributions (e.g., Dominance Decay and MacArthur Fraction models; Fig. 1), and might therefore be more difficult to discriminate compared to models with very dissimilar apportionment and/or breakage rules (e.g., Dominance Decay and Dominance Preemption models; Fig. 1).

As demonstrated in Table 1 and the examples above, sequential niche apportionment models are characterized by both stochastic and deterministic components. Thus, many different realizations of communities that conform to a particular model are possible (Pielou 1975), reflecting the inherent variability of natural systems. Yet, the expected relative abundance distributions that emerge over many realizations are quite distinct (Fig. 1). The issue, therefore, becomes whether or not these last two points can be reconciled; e.g., will an *individual* Dominance Decay community tend to be recognized as being best fit by the predictions of the Dominance Decay model (rather than some other model)? More generally, can past structuring processes of sequential niche apportionment be elucidated from present community relative abundance

patterns? My purpose here is not to debate the merits of the theoretical underpinnings of niche apportionment models themselves (i.e., I do not deal with the question of whether the apportionment and breakage rules are ecologically realistic), but rather to deal with the more practical issue of discriminating among a given set of potential apportionment processes from the relative abundance patterns they produce.

Wilson (1993) dealt with the specific case of distinguishing the MacArthur Fraction model (referred to in his analysis and elsewhere as 'Broken Stick') from other, statistically-based models (General Lognormal, Geometric Series and Zipf-Mandelbrot). By using Monte Carlo methods (Gotelli and Graves 1996) to generate many random 'communities' each conforming to the assumptions of the MacArthur Fraction model, Wilson demonstrated the following: (1) MacArthur Fraction random communities composed of fewer than approximately 20 species were more likely to be best fit by another model (in particular the General Lognormal model), rather than the MacArthur Fraction model. (2) As random communities with more and more species were examined, the probability that MacArthur Fraction random communities would be correctly identified marginally increased, accompanied by a decrease in the variance of the predicted relative abundance distributions with increasing species richness.

Wilson et al. (1998) performed additional analyses using a different suite of models (MacArthur Fraction ['Broken Stick'], Sequential Breakage [which converges on General Lognormal] and Randomized Niche Preemption [which converges on Geometric]). Similar conclusions to Wilson (1993) were drawn, with the likelihood of correctly identifying the provenance of a random community being very low in species-poor communities, but increasing in communities with more species.

Here, I applied the same logic to five major niche apportionment models (Table 1), to determine whether or not the relative abundance patterns of random communities tended to be best fit by the models whose assumptions were used to generate them (as would be predicted if current patterns can be used to hind-cast past processes), and whether or not this trend was affected by the number of species present in these random communities (see Mouillot and Wilson 2002, for a parallel approach using species evenness as a proxy for relative abundance distributions).

I also used an example situation from the literature (Bersier and Sugihara 1997) to examine the possibility that relative abundance distributions averaged from several replicated communities might be easier to distinguish than those derived from individual communities (Mouillot and Wilson 2002). While Wilson (1993) pointed out that replicate communities are difficult to find and are typically composed of inconsistent numbers of species, such a procedure has been attempted previously (e.g., Bersier and Sugihara 1997, Cassey and King 2001). Together, the results of these two sets of analyses are highly relevant to real communities, because they provide a method to estimate the confidence that a community structured by one of several possible niche apportionment processes will be correctly identified, given a particular level of community species richness and community replication.

## Methods

I followed a procedure similar to that of Wilson (1993) and Wilson et al. (1998). For each of the Dominance Decay, MacArthur Fraction, Random Fraction, Random Assortment and Dominance Preemption models, I generated 1999 random four-species 'communities' according to the appropriate apportionment and breakage rules (Table 1) using Monte Carlo randomization methods (Gotelli and Graves 1996; all analyses were performed on Visual Basic Editor of Microsoft Excel). I then compared the species' relative abundance distributions of these random communities against those of the expected communities (i.e., the relative abundance distributions that emerge over many replications; Fig. 1) for each of the

same five models by calculating the sum-of-squares of the log deviances (Wilson 1991); lower sums-of-squares corresponded to better fitting models. Log deviances were used so that abundant species did not dominate the fitting. (Because relative, rather than absolute abundance values were used, the mean relative abundance over all species was automatically fit in accordance with Wilson (1991). The mean relative abundance was always equal to one divided by the species richness of the random community). Other fitting criteria are possible, most notably the goodness-of-fit test proposed by Bersier and Sugihara (1997) and modified by Cassey and King (2001). This test has the advantage of being able to test both the mean and variance of a real data set against those predicted by the models, while Wilson's test only examines means. However, as a goodness-of-fit test, it is unsuitable for the question of distinguishing models (which requires a best-fit test such as Wilson's). For example, a series of goodness-of-fit tests on a particular relative abundance distribution data set might accept the Random Fraction model and reject the Dominance Decay model at a certain confidence level, yet it does not follow that the Random Fraction model fit the data significantly better than the Dominance Decay model. Similarly, another series of goodness-of-fit tests on a different relative abundance distribution data set might accept both the MacArthur Fraction model and the Dominance Preemption model, even though one provided a significantly better fit than the other. Hence, I followed Wilson's (1991) method instead.

Thus, for every random community type, I was able to determine whether the model used to generate it actually provided a better fit of relative abundances (over 1999 random communities) than any of the other models examined. The resulting frequencies of 'appropriate' best-fit were equivalent to the probabilities of correctly identifying the different types of communities.

I then repeated the entire procedure for communities of eight, 12, 16, 20, 24 and 28 species in order to determine whether there was a greater likelihood of correctly distinguishing communities of increasing species richness (as was shown for the MacArthur Fraction model by Wilson 1993 and for other models by Wilson et al. 1998).

To investigate whether or not averaging replicated communities made them easier to correctly identify, I generated a further 1999 random data sets of four-species communities for each of the same five sequential niche apportionment models. For this set of analyses, each data set was calculated as the average relative abundance distribution of seven replicate random communities; thus, 13993 (i.e., 1999 x 7) additional realizations of random communities generated by each model were required. The

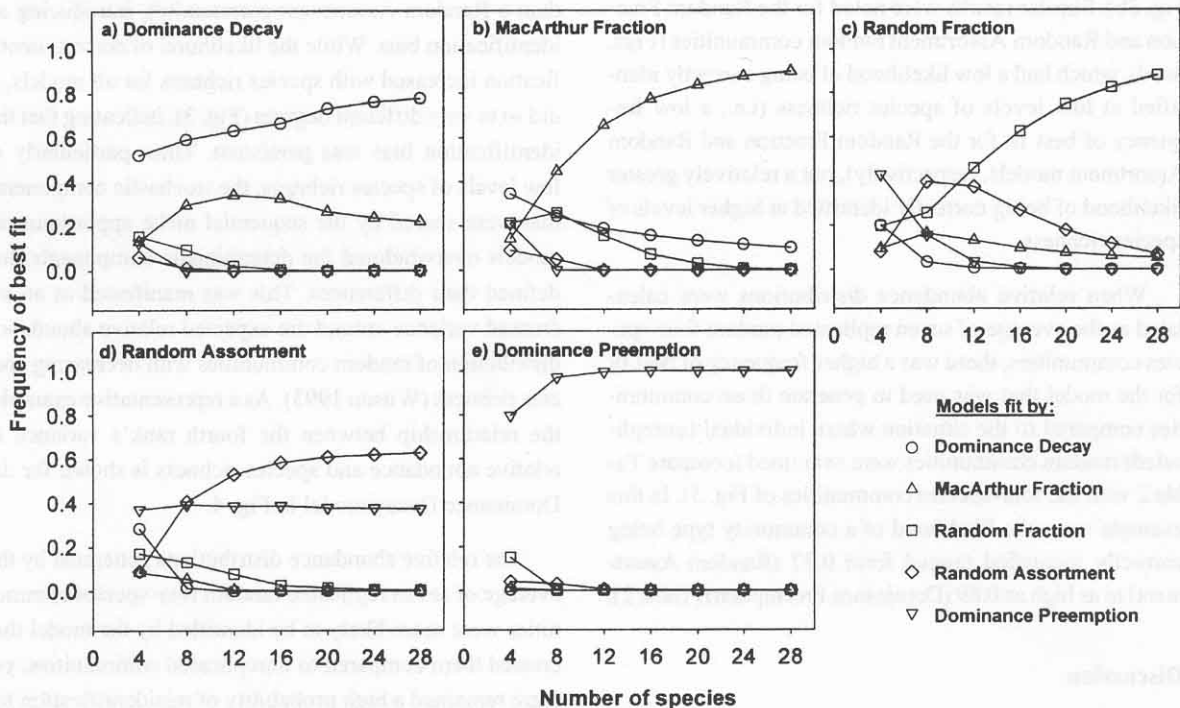
reason I specifically examined the case of seven replicates of a four-species community was to mirror the conditions of a previously published data set (Bersier and Sugihara 1997). Of course, this is only one example, and in practice, this decision should be made on a case-by-case basis, taking into account the number of replicate communities available and their species richness values for the system of interest. I tested the 1999 average relative abundance distributions of the five different data set types (Dominance Decay, MacArthur Fraction, Random Fraction, Random Assortment, Dominance Preemption) against the expected relative abundance distributions of those same models with the same criterion as above (sum-of-squares of log deviances), in order to determine the effect of using replicated, rather than individual communities in this example.

## Results

For the Dominance Decay random communities (Fig. 3a), the Dominance Decay model provided the best fit most of the time for all levels of species richness. The frequency of best fit (indicating the proportion of instances that the past structuring processes were correctly identified) increased steadily from 0.52 in four-species commu-

nities to 0.78 in 28-species communities. Thus, in four-species communities, the odds of correctly identifying a Dominance Decay community were slightly better than one-to-one. Similar results were noted for the Dominance Preemption random communities (Fig. 3e), although the frequency of best fit of the Dominance Preemption model was greater, rapidly increasing from 0.80 (four-species communities) to 1.0 (28-species communities).

The other three types of random communities examined (MacArthur Fraction, Random Fraction and Random Assortment) were much more difficult to correctly identify at low levels of species richness (i.e., fewer than 12 species) than the Dominance Decay and Dominance Preemption random communities. For MacArthur Fraction random communities, the frequency of best fit of the MacArthur Fraction model was 0.14 in four-species communities (Fig. 3b). At this low level of species richness, it was actually more likely that the Dominance Decay, Random Fraction and Dominance Preemption models would give a better fit than the MacArthur Fraction model that was used to generate the random communities in the first place. As more species were present in the community, this trend changed and the MacArthur Fraction model emerged as providing the best fit most of the time (with a



**Figure 3.** Frequency of best fit (least sum-of-squares of log deviances) of the Dominance Decay model (circles), MacArthur Fraction model (upward triangles), Random Fraction model (squares), Random Assortment model (diamonds) and Dominance Preemption model (inverted triangles) when applied to random communities of varying species richness generated by the assumptions of those same models. For each random community type [a) Dominance Decay, b) MacArthur Fraction, c) Random Fraction, d) Random Assortment, e) Dominance Preemption] at each level of species richness (four, eight, 12, 16, 20, 24, 28), 1999 random communities were used.

**Table 2.** Frequencies of best fit (least sum-of-squares of log deviances) for five models of sequential niche apportionment, Dominance Decay (DD), MacArthur Fraction (MF), Random Fraction (RF), Random Assortment (RA) and Dominance Preemption (DP), when applied to random data sets derived from those same five models. Each random data set was the average of seven random four-species communities, in order to mirror the data structure of Bersier and Sugihara (1997). 1999 such data sets were used for communities of each model. Each type of random data set was best fit most of the time by the model used to generate it, as indicated by the numbers in boldface.

Model fit best by	Random data set type				
	DD	MF	RF	RA	DP
DD	<b>0.63</b>	0.25	0.03	0.05	0.00
MF	0.26	<b>0.44</b>	0.20	0.29	0.00
RF	0.04	0.12	<b>0.42</b>	0.28	0.07
RA	0.07	0.19	0.35	<b>0.37</b>	0.03
DP	0.00	0.00	0.00	0.00	<b>0.89</b>
Sum	1.00	1.00	1.00	1.00	1.00

frequency of best fit of 0.90 in 28-species communities; Fig. 3b). Similar results were noted for the Random Fraction and Random Assortment random communities (Figs. 3c, d), which had a low likelihood of being correctly identified at low levels of species richness (i.e., a low frequency of best fit for the Random Fraction and Random Assortment models, respectively), but a relatively greater likelihood of being correctly identified at higher levels of species richness.

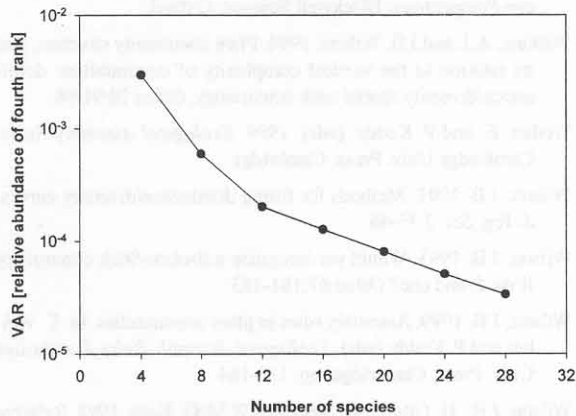
When relative abundance distributions were calculated as the average of seven replicated random four-species communities, there was a higher frequency of best fit for the model that was used to generate those communities compared to the situation where individual (unreplicated) random communities were examined (compare Table 2 with the four-species communities of Fig. 3). In this example case, the likelihood of a community type being correctly identified ranged from 0.37 (Random Assortment) to as high as 0.89 (Dominance Preemption) (Table 2).

## Discussion

For species-poor, unreplicated communities, there was a high probability of misidentifying the model that gave rise to any particular random community type (Fig. 3). This problem was compounded by the fact that the likelihood of correct identification was inconsistent across the different models (e.g., it was much more likely

to correctly identify a Dominance Preemption community than a Random Assortment community), introducing an identification bias. While the likelihood of correct identification increased with species richness for all models, it did so to very different degrees (Fig. 3), indicating that the identification bias was persistent. Thus, particularly at low levels of species richness, the stochastic components that were shared by the sequential niche apportionment models overwhelmed the deterministic components that defined their differences. This was manifested as an increased variance around the expected relative abundance distribution of random communities with decreasing species richness (Wilson 1993). As a representative example, the relationship between the fourth rank's variance in relative abundance and species richness is shown for the Dominance Decay model in Fig. 4.

The relative abundance distributions generated by the average of seven replicated random four-species communities were more likely to be identified by the model that created them compared to unreplicated communities, yet there remained a high probability of misidentification for some models (Table 2). Hence, in this example scenario (analysing the data structure of Bersier and Sugihara 1997), it is quite likely that a large proportion of the community types were misidentified. Moreover, the likelihood of correct identification remained inconsistent across models (Table 2), indicating that the identification



**Figure 4.** Variance in relative abundance of the fourth rank of random Dominance Decay communities with respect to species richness. For each level of species richness (four, eight, 12, 16, 20, 24, 28) 1999 random communities were used. Results for other ranks and models were similar (not shown).

bias continued to persist at this level of community replication.

These results have clear implications for studies examining natural communities. They indicate that in a community of low species richness (and/or low levels of community replication), there is no way to speculate from current relative abundance patterns alone which (if any) niche apportionment processes were previously at work. As communities with more species are examined, or more replicate communities are incorporated into the analysis (Cassey and King 2001, Mouillot and Wilson 2002), the process of distinguishing among different types of communities becomes more certain, but there may still be a high probability of misidentification. Therefore, in the endeavour of discriminating among community types, it appears as though the use of sequential niche apportionment models must be confined to situations where the combination of the species richness and the number of replicated communities is sufficiently great to allow for the resolution of the different models. Individual studies can use the methods described here to determine the likelihood of correctly identifying community types based on the species richness and level of replication available for the system of interest (see also Mouillot and Wilson 2002). This would be done for similar reasons as *a priori* power analysis - to determine whether the test is capable of doing what it purports to do, in this case discriminating among models. Unfortunately, it is difficult in practice to increase richness and replication simultaneously, since the replication of communities with the same number of

species will become more difficult as species richness increases.

Other important issues must be considered when attempting to understand niche apportionment processes and relative abundance patterns. For example, although I chose to examine five major sequential niche apportionment models, others are possible merely by setting new apportionment and breakage rules. Consider a hypothetical niche apportionment process for which the apportionment rule is 'random' and the breakage rule is 'fragment to be broken next chosen at random, weighted inversely by fragment size'. This 'Inverse MacArthur Fraction' model, as it might be called, would produce similar relative abundance distributions to those generated by the Dominance Preemption model in the same way that the original MacArthur Fraction model produced distributions similar to those generated by the Dominance Decay model (Fig. 1). This similarity would lead to mutual misidentification of communities produced by the Inverse MacArthur Fraction and the Dominance Preemption models, just as MacArthur Fraction and Dominance Decay communities were frequently confused with one another (Figs. 3a, b). Thus, as more models are incorporated into an analysis, and the differences among models become even more subtle, the problem of identifying the appropriate sequential niche apportionment process must necessarily become even more severe. Given this continuum of community types, perhaps emphasis should shift from attempts to fit community types into discrete categories (as was the case here and in the other recent studies), and instead focus on describing community types based on their position in the continuum. An additional technical difficulty concerns 'composite' models of sequential niche apportionment (Tokeshi 1990). There is no theoretical reason to expect that an entire community, from abundant to rare species, should be governed by one model. Finally, the model providing best fit to a particular community is likely highly dependent on the spatial scale of sampling (Wilson et al. 1998). The determination of past niche apportionment from current abundance patterns continues to be an important challenge in community ecology.

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## References

- Bersier, L.-F. and G. Sugihara. 1997. Species abundance patterns: the problem of testing stochastic models. *J. Anim. Ecol.* 66:769-774.

Cassey, P. and R.A.R. King. 2001. The problem of testing goodness-of-fit of stochastic resource apportionment models. *Environmetrics* 12:691-698.

Fisher, R.A., A.S. Corbet, and C.B. Williams. 1943. The relationship between the number of species and the number of individuals in a random sample from an animal population. *J. Anim. Ecol.* 12:42-58.

Gotelli, N. J. and G.R. Graves. 1996. *Null Models in Ecology*. Smithsonian Institution Press, Washington.

MacArthur, R. H. 1957. On the relative abundance of bird species. *Proc. Natl. Acad. Sci. USA* 43:293-295.

Mouillot, D. and J.B. Wilson. 2002. Can we tell how a community was constructed? A comparison of five evenness indices for their ability to identify theoretical models of community construction. *Theor. Popul. Biol.* 61:141-151.

Pielou, E.C. 1975. *Ecological Diversity*. Wiley, New York.

Preston, F.W. 1948. The commonness and rarity of species. *Ecology* 29:254-283.

Tokeshi, M. 1990. Niche apportionment or random assortment: species abundance patterns revisited. *J. Anim. Ecol.* 59:1129-1146.

Tokeshi, M. 1993. Species abundance patterns and community structure. *Adv. Ecol. Res.* 24:111-186.

Tokeshi, M. 1999. *Species Coexistence: Ecological and Evolutionary Perspectives*. Blackwell Science, Oxford.

Watkins, A.J. and J.B. Wilson. 1994. Plant community structure, and its relation to the vertical complexity of communities: dominance/diversity spatial rank consistency. *Oikos* 70:91-98.

Weiher, E. and P. Keddy. (eds). 1999. *Ecological Assembly Rules*. Cambridge Univ. Press, Cambridge.

Wilson, J.B. 1991. Methods for fitting dominance/diversity curves. *J. Veg. Sci.* 2:35-46.

Wilson, J.B. 1993. Would we recognize a Broken-Stick community if we found one? *Oikos* 67:181-183.

Wilson, J.B. 1999. Assembly rules in plant communities. In: E. Weiher and P. Keddy (eds), *Ecological Assembly Rules*. Cambridge Univ. Press, Cambridge, pp. 130-164.

Wilson, J.B., H. Gitay, J.B. Steel and W.McG. King. 1998. Relative abundance distributions in plant communities: effects of species richness and of spatial scale. *J. Veg. Sci.* 9:213-220.

Wilson, J.B., T.C.E. Wells, I.C. Trueman, G. Jones, M.D. Atkinson, M.J. Crawley, M.E. Dodd and J. Silvertown. 1996. Are there assembly rules for plant species abundance? An investigation in relation to soil resources and successional trends. *J. Ecol.* 84:527-538.